RAPTOR RESEARCH

Volume 14
Number 3
Fall 1980

Raptor Research Foundation, Inc.
Provo, Utah, U.S.A.

RAPTOR RESEARCH Fall 1980
Volume 14, Number 3, Pages 65–96

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RAPTOR RESEARCH

Published Quarterly by the Raptor Research Foundation, Inc.

Editor Dr. Clayton M. White, Dept. of Zoology, 161 WIDB, Brigham Young University, Provo, Utah 84602
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IDENTIFICATION OF THE SEX CHROMOSOMES OF THE RED-TAILED HAWK (*BUTEO JAMAICENSIS*) BY C- AND G-BANDING

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Abstract

We analyzed the mitotic chromosomes from a Red-tailed Hawk using G- and C-banding techniques. We found the Z chromosome to be the largest and the W chromosome to be the eighth largest. Other chromosomal characteristics and possible causes for incorrect sex chromosome identification in earlier reports are discussed.

Introduction

The difficulties encountered by aviculturists in accurately determining the sex of many captive birds has been one of the basic problems impeding efforts aimed at reproducing rare forms in captivity. Pape and Ogasawara (1978) indicate, in their study of the karyotype of the Red-tailed Hawk (*Buteo jamaicensis*), that captive birds of prey are not always easy to sex. They used feather pulp to obtain chromosome preparations and by analysis of such undifferentially stained preparations were able to sex their captive birds.

The technique of chromosome banding yields much more reliable data on sex chromosomes and chromosome homologies. Since the chromosomes they selected as representing the Z and W chromosomes (fourth largest chromosome pair) did not correspond to those published for raptors by Takagi and Sasaki (1974), Kaul and Ansari (1975), and Mengden and Stock (1976), we analyzed the C- and G-banded chromosomes of the Red-tailed Hawk to identify the actual sex chromosomes in that species.

Materials and Methods

Pinfeathers were removed from a recently road-killed Red-tailed Hawk. Preparation of chromosome spreads from the feather pulp tissue followed the squash technique of Mengden and Stock (1976). Some pulp tissue was cultured to obtain cell harvests high in mitotic index (Stock and Mengden 1975). Usable material was obtained by both direct squash and culture methods although the quality of banding was much better with material from cell culture. G-banding followed the procedures of Stock et al. (1974). C-banding was accomplished by the alkaline SSC method of Stefos and Arrighi (1971).

Results

Counts from 20 well-spread metaphase complements indicate a 2n of 68. Analysis of G-banded metaphase chromosomes (fig. 1) indicates the largest chromosome of the complement lacks a banding pattern homologue. The eighth largest chromosome in the

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complement also lacks a matching homologue. All other chromosome pairs can be matched. C-banded metaphase chromosomes (fig. 2) show the largest chromosome to be the Z and the eighth largest chromosome to be the W chromosome (which is almost entirely heterochromatic and is easily recognizable). Most autosomes possess some heterochromatin near the centromere although a few pairs, especially the larger ones, possess very little heterochromatin. The six smallest pairs of chromosomes are largely heterochromatic. Chromosome pair #4 in the G-banded karyotype possesses a large nonstaining region on the short arm near the centromere; and C-banding (fig. 2) reveals a large block of heterochromatin near the centromere. Much of the nonstaining region on chromosome #4, however, is distal to the heterochromatic region. This pair of chromosomes often shows an end-to-end association, hence the nonstaining region probably represents a nucleolar organizer region (NOR).

Discussion

The count of 34 pairs of chromosomes (2n = 68) reported by Pape and Ogasawara (1978) for the species is supported by this study. Almost all metaphase spreads counted possessed this number. Random loss of chromosomes during preparation accounted for the few lower counts obtained. Raptors usually possess fewer chromosomes than is the case in most other bird groups. Even with their reduced number of chromosomes, however, matching by centromeric index is difficult because of differential contraction of homologues. Selection of the wrong chromosomes as sex chromosomes is typical of errors that can result from the use of non-differentially stained chromosomes.

In cases where the W chromosome is large (many raptors), mistakes are frequent and may cause one to assume the wrong sex for the bird being studied. The feather-pulp method (Mengden and Stock 1976, Pape and Ogasawara 1978), combined with C-banding techniques, accurately determines a bird's sex. Such methodology can be employed with a minimum of expense and time and yields far more reliable information than do techniques such as laparotomy or analysis of fecal steroids (Risser 1977). The use of C-banding precludes the laborious task of obtaining centromeric index data and arranging the chromosomes into a karyotype as one can observe the W chromosome, if present, very readily in the spread of metaphase chromosomes. It may be possible to detect the W chromosome heterochromatin in interphase cells in species where the amount of autosomal heterochromatin does not interfere with clear visualization of the W-body (Stefos and Arrighi 1971).

The use of a mitotic arrester, such as colcemid, by direct injection into the bird, is not a good practice and may damage the bird by producing chromosomal abnormalities such as tetraploidy in cells blocked at metaphase. The resultant effects on breeding birds should be avoided. The practice is not necessary as the mitotic arrester can be successfully used in the hypotonic treatment (Mengden and Stock 1976) in the case of pinfeathers or prior to harvest in the case of cell culture.

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Takagi, N., and M. Sasaki. 1974. A phylogenetic study of bird karyotypes. *Chromosoma* 46:91–120.

Ed. Note: Sample size is reportedly not a concern in studies of this type.

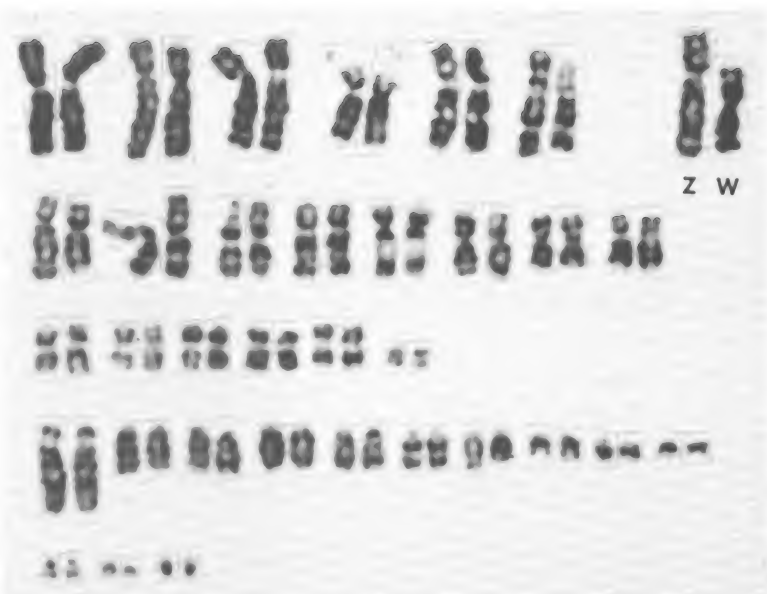

Figure 1. G-banded karyotype of the Red-tailed Hawk.

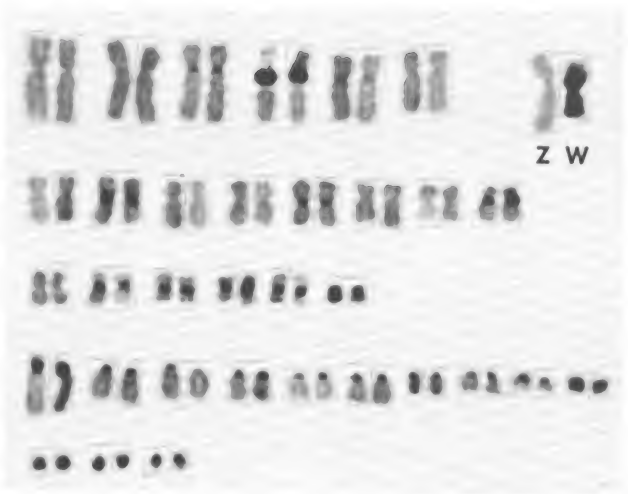

Figure 2. C-banded karyotype of the Red-tailed Hawk.

THE NESTING OF AN ALBINISTIC RED-TAILED HAWK (*BUTEO JAMAICENSIS*) IN OREGON

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Although albinism among Red-tailed Hawks (*Buteo jamaicensis*) has been reported (Emerson 1897, Ross 1963, Gross 1965, West 1971, Melquist and Shroeder 1974, Eckert 1974, Harris 1977, Follen 1979), there are few reports of the pairing and nesting of albinistic Red-tailed Hawks. Emerson (1897) stated that the albinistic bird he observed was paired, but he was unable to locate the nesting site. Recently Follen (1979) reported the pairing of an albinistic Redtail, but he gave no information whether nesting occurred.

Because of the lack of data regarding the nesting of albinistic Red-tailed Hawks, and also because of the supposed rarity of albino western Redtails (Austing 1964, Melquist and Shroeder 1974), we believe the following information to be noteworthy.

An albinistic male Red-tailed Hawk was observed by us every month from April 1977 to May 1979 and had been reported in the area by competent observers since 1972. This bird occupied a nesting territory in a second growth Douglas fir (*Pseudotsuga menziesii*) forest bordering farmland approximately 6.5 km southwest of Philomath, Benton County, Oregon (section 28, T.12S, R.6W, 230 m elevation). The hawk was almost completely white except for a slight reddish tint on the rectrices and a few dark-tipped feathers on the breast, nape, and rear of the crown. The beak appeared to have normal coloration and the eyes appeared dark (fig. 1). Using the terminology of Pettingill (1970), we would classify this buteo as an imperfect albino. The pigment was reduced or diluted in the plumage but was not completely absent.

This imperfect albino nested with a normally pigmented female in 1977 and 1978. In the spring of 1978, nuptial displays occurred in late February and early March. Both birds constructed the nest approximately 25 m high in a Douglas fir tree. Copulation was observed on 15 March and on several occasions shortly thereafter. Incubation started on 1 April and was subsequently carried on by both parents. Young were seen in the nest on 15 May. All of the young were of normal plumage, as was the case in 1977. During the incubation and nestling period, the male, on several occasions, chased a normal-colored, immature Redtail from the nest area. The pair did not use the same nest in 1979, and we do not know whether they nested again or not.

Sage (1962) reported that albinism in birds may be either congenital, in which case it is recessive; or environmental, in which case it is due to factors such as diet, injury, shock, or disease. In either case it is not surprising that the offspring of this albino male have not exhibited any of his color characteristics. However, we believe it is significant that a bird of this coloration has survived so long in the wild and has nested successfully.

We thank Eric Forsman for his review and comments on this note.

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Figure 1. Imperfect albino Red-tailed Hawk perched near nest tree in Benton County, Oregon.

SURVIVAL OF THE SMALLEST NESTLING IN GOSHAWKS

by
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Abstract

A nest containing four Goshawk chicks was observed during the 1979 breeding season. One young was smaller than its siblings throughout most of the nestling period. It called more during feedings and received less food. The adult female varied in her response to the small bird as the season progressed. She ignored calls early in the season, yet the young hawk was fed in the nest after all other chicks had flown. Possible reasons for this contradiction in adult behavior and its relation to food supply are discussed.

Introduction

Asynchronous hatching can be regarded as an adaptation to an unpredictable food supply, enabling all young to survive in times of plenty, but ensuring rapid reduction of the brood to an appropriate level in times of scarcity (Newton 1978a). This paper documents the survival of a young Goshawk (*Accipiter gentilis*) despite a 1–3 day age difference at hatching among the four chicks and an 18-day difference in dates of leaving the nest from first to last young. Lack (1968) stated that it is probably important for young

birds all to leave the nest at the same time if continued feeding by the parents occurs. Apparently young Goshawks can be fed despite leaving the nest at different times.

Study Area

Data on breeding behavior of Goshawks were collected from 6 March–1 August 1979 on an 800 ha area, 24 km north of Provo, Utah. Elevation ranges from 1991 to 2195 m. Approximately 80 percent of the area is forested, predominately aspen (*Populus tremuloides*) with some mixed forest including white fir (*Abies concolor*) and Rocky Mountain Douglas fir (*Pseudotsuga menziesii*). Observations were made from a tree blind 27.4 m west of the nest that was located in an aspen 9 m from the ground and were made in the course of the breeding study.

Results and Discussion

Four young hatched by 8 June with a 1–3 day age spread among them. By 16 June one was estimated to be half the length of the other nestlings. It begged for food intermittently as the others slept. At each feeding the larger chicks pulled food from the mouth of the hen as soon as it was presented. If food was not taken immediately from her beak, the female fed herself.

Newton (1978b) stated that one factor in assuring an even growth rate among Sparrowhawk (*Accipiter nisus*) nestlings is the sharing of prey by the female until a late stage in nestling growth. The female Goshawk made no attempt to feed the smallest chick selectively although the young bird continued to call when all other young were silent after feeding. Newton (1976) suggested that a single young may present to the hen an insufficient stimulus for feeding. Although the brood consisted of four chicks, the smallest was the only one that called at the end of a meal. The calls apparently were not sufficient to induce the hen to continue feeding the young. At the end of each meal the small chick had a partially filled crop compared to the full crops of its siblings. It obtained much of its food by taking it from the beak of a larger nestmate.

Lack of food partitioning led to the death of several nestling Marsh Hawks (*Circus cyaneus*) (Breckenridge 1935). Newton (1976) and Mebs (1964) found that a cannibalism or death of the smallest chick was a consequence of underfeeding in Sparrowhawks and the Common Buzzard (*Buteo buteo*), respectively. Ingram (1959) cites fratricide often followed by cannibalism in Goshawks. During the current study, an attack by a larger nestmate was observed on only one occasion in the second week after hatching.

The smallest chick was less than half the size of it nestmates by 27 June when I banded them and still had no pinfeathers while the others were beginning to lose down. One chick had left the nest by 13 July, and two were found sitting on branches adjacent to the nest. Only the smallest chick remained in the nest on 26 July. Feathers had grown, and down was visible only on the legs and abdomen and under the wings. The bird had moved to the branches on 31 July and flew first on 1 August. The adults had continued to feed it in the nest while also feeding chicks that had already flown from the nest.

The parents would gain inclusive fitness by retaining or even becoming more sensitive to care-soliciting behavior in young birds nearly ready to fly. The adults had a greater investment in terms of time, care, and energy in their young late in the nestling stage. Had the smallest chick died soon after hatching, the loss would not have been as great. Since the adults had expended energy and time to raise the young hawk to four weeks, the advantage was to respond to calls of the smallest chick rather than to allow it to die.

One additional offspring in the population would increase the genetic potential of the adult Goshawks.

Prey were abundant in the 1979 nesting season. Food items included the Uinta ground squirrel (*Spermophilus armatus*), Steller's Jay (*Cyanocitta stelleri*), and Common Flicker (*Colaptes auratus*). Small mammal density was estimated by the recapture method (Smith et al. 1972, Scott et al. 1978), and was 165 animals per hectare in the meadows surrounding the nest woodlot. If food had been in short supply, there would have been no fitness gained by raising four undernourished young that would never survive to reproduce. At the other extreme, there would have been considerable waste of parental investment by having neglected a chick that could have been adequately fed.

Acknowledgments

Robert Redford, Dale and Jeanne Quesenbury, Sarah A. Lee, and Brigham Young University Zoology Department funded the study. Field and other assistance were provided by B. Beck, H. Black, T. Cade, D. Carr, C. Elliott, J. Flinders, D. Johnson, L. Klein, J. Murphy, P. Murphy, A. Nelson, M. Shindurling, Sundance Ski Resort, K. VanDeGraaff, and C. White.

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ANNOUNCEMENT

SPECIAL ISSUE OF RAPTOR RESEARCH DEVOTED TO GOLDEN EAGLES

The Raptor Research Foundation, Inc., will devote the spring issue, 1982, of *Raptor Research* to publishing significant new research on golden eagles. Full length manuscripts as well as shorter communications are being actively solicited. The deadline for manuscripts is 1 July 1981. For further information please contact Richard L. Knight, Washington Eagle Study, Washington Department of Game, 600 N. Capitol Way, Olympia, WA 98504.

Figure 1. One-month-old Goshawk chicks. The adult female is in the background.

FEEDING ECOLOGY OF THE SPOTTED OWL IN CALIFORNIA

by
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Abstract

The Spotted Owl (*Strix occidentalis*) from the Coast Range of northern California and the Peninsular Range of southern California preys heavily on forest-dwelling mammals, especially the dusky-footed woodrat (*Neotoma fuscipes*). Meadows are not regularly hunted by these owls, despite large numbers of prey there. Indexes of prey biomass diversity indicate a relatively narrow prey base for the Spotted Owl in California. The Screech Owl (*Otus asio*) is an uncommon but regular prey item of the Spotted Owl; mobbing by Screech Owls in response to imitated Spotted Owl calls is described.

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Introduction

Forsman (1975) provided a very complete analysis of Spotted Owl (*Strix occidentalis*) prey in Oregon, but comprehensive regional food data from other locations are nearly absent. Prior to Forsman's study, Marshall (1942) reported prey contents of two Spotted Owl stomachs together with several pellets from one location in the Sierra Nevada, California, and three owl stomach contents from the northern Cascades, Oregon. Other published accounts have described less than 20 prey items from a single location, in most cases from only one stomach (Richardson 1906; Daggett 1913; Dickey 1914; Huey 1932; Miller 1933; Johnson and Russell 1962; Smith 1962; Maser 1965; Kertell 1977).

I present prey data from nine pairs of Spotted Owls in California. These data are then compared to those presented by Forsman (1975) for Oregon. Measures of prey species diversity and biomass diversity are also considered. This comparison permits the elucidation of patterns in Spotted Owl prey selection over a wide geographic area.

Study Site and Methods

Prey data from the North Coast Range of northern California were gathered from four pairs of Spotted Owls from June through August 1977. Two pairs were in the Nature conservancy's Northern California Coast Range Preserve, Mendocino County. Another pair was on Point Reyes Peninsula, Marin County, and a fourth pair at San Geronimo, Marin County.

In the Peninsular Range of southern California data were collected from five pairs of owls between June 1978 and November 1979: one pair each in the San Jacinto Mountains, Riverside County; Santa Ana Mountains, Orange County; Palomar Mountain, San Diego County; and two pairs in the Cuyamaca Mountains, San Diego County.

Vegetation at all locations was typical of the mixed evergreen forest (Sawyer et al. 1977). A more complete description of the habitat characteristics at each site is given in Barrows and Barrows (1978) and Barrows (1980).

All prey items identified were recovered from Spotted Owl pellets, totalling 250 pellets from the North Coast Range and 200 pellets from the Peninsular Range. The accuracy of using owl pellets in a determination of prey consumption was discussed by Errington (1930). Mammalian prey items were identified using the keys of Ingles (1965) and Glass (1973). Small mammal densities in meadows were estimated by observing visual signs of activity (i.e., runways). Other prey species were identified by comparison with museum specimens and, in the case of insects, with living individuals. Prey weight measurements used in the calculation of percent biomass are from Forsman (1975). Prey biomass diversity was calculated as the product of the number of individuals of a particular species multiplied by that species' mean weight.

Results and Discussion

The prey species and their relative proportion in the Spotted Owls' pellets are shown in table 1. Calculations of percent biomass are also included as a more descriptive measure of the value of each prey species in meeting the owls' energetic requirements. Table 1 shows two major trends: there is a clear preference by the owls for forest-dwelling species; and the dusky-footed woodrat (*Neotoma fuscipes*) accounts for a significant proportion of the total biomass consumed by Spotted Owls.

The only nonforest species listed in table 1 is the California meadow mouse (*Microtus californicus*) whose preferred habitat is meadows. Spotted Owl hunting ranges occasionally encompassed meadows which were found to harbor large numbers of meadow mice.

Table 1. Spotted Owl Prey Items from the North Coast and Peninsular Mountain Ranges of California.

Species	North Coast Range (N = 375) N	Percent Occurrence	Percent Biomass	Peninsular Range (N = 296) N	Percent Occurrence	Percent Biomass
Mammals						
Neotoma fuscipes	112	29.9	69.2	98	33.1	79.3
Arborimus longicaudus	64	17.1	4.0	0	0.0	0.0
Glaucomys sabrinus	56	14.9	14.8	0	0.0	0.0
Peromyscus sp.	48	12.8	2.4	91	30.7	6.0
Scapanus latimanus	4	1.1	0.5	1	0.3	0.2
Microtus californicus	2	0.5	0.1	3	1.0	0.2
Lasiurus cinereus	2	0.5	0.05	0	0.0	0.0
Mustela erminea	1	0.3	0.1	0	0.0	0.0
Sylvilagus sp.	1	0.3	0.8	1	0.3	1.0
Eutamias sp.	1	0.3	0.2	1	0.3	0.2
Thomomys bottae	0	0.0	0.0	23	7.8	6.0
unident. mammals	2	0.5	0.1	0	0.0	0.0
Birds						
Cyanocitta stellari	10	3.1	2.7	5	2.1	2.0
Otus asio	5	1.3	1.6	3	1.0	1.3
Glaucidium gnoma	1	0.3	0.1	0	0.0	0.0
other birds[a]	21	5.6	3.4	18	6.1	3.8
Arthropods[b]	45	12.0	0.2	52	17.6	0.3

a. Includes *Melanerpes formicivorus, Colaptes auratus, Turdus migratorius, Junco hyemalis,* unidentified species.

b. Includes largely insects (Orthoptera, Coleoptera), with a minor representation of Scorpionida and Diplopoda.

The low numbers of this species in Spotted Owl pellets in both regions suggest that the owls rarely hunt in such open areas. My observations of Spotted Owls during twilight hours showed them to hunt exclusively from elevated perches; the absence of such perches in open meadows may account for their low utilization of these areas.

The remaining prey species commonly inhabit forested areas. Of these species, the dusky-footed woodrat, the western flying squirrel (*Glaucomys sabrinus*), the red-backed tree mouse (*Arborimus longicaudus*), and the deer mouse (*Peromyscus* sp.) make up the largest portion of the diet in areas examined.

In the North Coast and Peninsular Ranges, California, and in the eastern Siskyou Mountains of southern Oregon (Forsman 1975), the dusky-footed woodrat comprises over 69 percent of the Spotted Owl prey biomass. In other regions of Oregon reported by Forsman (1975) the dusky-footed woodrat constitutes only a minor portion, or is absent, as a prey item in the Spotted Owls' diet. In those regions, the flying squirrel and the bushy-tailed woodrat (*Neotoma cinerea*) were the most common prey species.

Prey diversity (table 2) gives a further characterization of the Spotted Owl's prey base. Numbers and proportions of prey species in each region are roughly similar, hence the consistent values for the species diversity index. However, prey biomass diversity index, which emphasizes relative mass of individual prey items, is lower for California areas and the eastern Siskyou Mountains than for any other Oregon sites. Lower prey biomass diversity values indicate a relatively narrow prey base, in this case a reflection

of the large numbers of heavy dusky-footed woodrats in the diet. Prey biomass diversity may be a more descriptive method of depicting the prey base because it does not compute a woodrat and a beetle to be of equal importance.

Table 2. Regional Comparison of Spotted Owl Prey Diversity.

Location	N	Prey Species Diversity[a]	Prey Biomass Diversity[a]
Oregon (7 areas)[b]	2,453	2.43–1.18	2.20–1.50
Oregon, eastern Siskyou Mountains[b]	176	1.81	1.02
Northern California Coast Range	375	1.97	1.15
Southern California Peninsular Range	296	1.62	0.87

a. Shannon-Wiener diversity index, H' = - pi log pi.

b. Calculated from Forsman 1975; (tables 1–8).

In regions where dusky-footed woodrats commonly occur, such as those reported from California and the eastern Siskyou Mountains, these mammals appear to be preferentially taken by Spotted Owls. Forsman (1975) suggested that Spotted Owls prey selectively on larger, arboreal mammals over more abundant, smaller, terrestrial species. It is unclear, however, whether it is larger size or semiarboreal habits or a combination of these factors that stimulate Spotted Owls to select such a high proportion of dusky-footed woodrats.

Future research might examine the possible relationship between woodrat populations and the reproductive biology and/or habitat selection of Spotted Owls in California. Other studies have revealed a correlation between prey numbers and the reproductive success of owls (Craighead and Craighead 1956; Southern 1970; Adamcik et al. 1978), and of other raptors (Hamerstrom 1979). Spotted Owls do not breed every year (Forsman 1975; Barrows unpubl. data). The dominance of woodrats in Spotted Owl diets from the areas reported in this study and the knowledge that woodrat populations can fluctuate greatly from year to year (Linsdale and Tevis 1951) suggest a possible cause and effect relationship in Spotted Owl breeding patterns.

Of the nonmammalian prey (table 1), the occurrence of the Screech Owl (*Otus asio*) in the Spotted Owls' diet warrants particular mention. So-called cannibalism by Spotted Owls was reported by Richardson (1906) and Daggett (1913) after finding remains of the Pygmy Owl (*Glaucidium gnoma*) in Spotted Owl stomachs. Forsman (1975) reported the Screech, the Pygmy, and the Saw-Whet Owl (*Aegolius acadicas*) as Spotted Owl prey items. While calling for Spotted Owls during summer nights, using vocal imitations of their calls, I was frequently "mobbed" by Screech Owls. Immediately following my imitation of a Spotted Owl call, Screech Owls in the near vicinity frequently began calling in a raucous, chattering manner. The Screech Owls were usually in family groups of one or two adults accompanied by several owlets. Both adults and immatures used the chattering calls. Adult Screech Owls moved sporadically through the trees surrounding me while calling; the owlets remained more or less stationary. The adult and immature

Screech Owls were easily located with a flashlight while engaged in this mobbing behavior. A high proportion of Screech Owl remains in the Spotted Owl pellets were recovered during July, the same period when the mobbing behavior of Screech Owl family groups was most pronounced. The chattering call by Screech Owls in response to a Spotted Owls' call was also heard, but at a lower intensity, throughout the late summer and fall months. The effect of the Screech Owls' mobbing behavior on Spotted Owls is unknown, but it certainly made my detection of these small owls easier.

Conclusions

General conclusions which can be drawn from this analysis of Spotted Owl feeding ecology are:

1. The owls' diet consists largely of forest-dwelling mammalian species, with prey items averaging more than 100 g.
2. Meadows or large open expanses were not regularly used by Spotted Owls for hunting, despite potentially large numbers of prey there.
3. When available, the dusky-footed woodrat comprises a high proportion of Spotted Owls' diet in California and may be preferentially selected by the owls.

I have no prey data from the Sierra Nevada or data on temporal variation in prey selection. The need for more data pertaining to the relationship between prey and Spotted Owl breeding patterns is discussed above. These gaps need to be filled before our knowledge of Spotted Owl feeding ecology is complete.

Acknowledgments

I wish to convey my appreciation for the use of the Nature Conservancy's Northern California Coast Range Preserve and Cuyamaca Rancho State Park as bases for my regional study. For their helpful comments on the manuscript, I thank Katherine Barrows and Charles Collins.

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ANNOUNCEMENTS

REQUEST FOR OBSERVATIONS

Please report any fall/winter sightings of adult Harlan's race Red-tailed Hawk (*Buteo jamaicensis harlani*). Include plumage description or photographs along with sighting locations. Historical information is also welcome.

Send information to: David Mindell, c/o Bureau of Land Management, 4700 E. 72nd, Anchorage, AK 99507.

CONFERENCE FOR INTERNATIONAL ASSOCIATION FOR FALCONRY AND CONSERVATION OF BIRDS OF PREY

The International Association for Falconry and Conservation of Birds of Prey is organizing a conference, 'Understanding the Goshawk', to be held in Oxford, Great Britain, from 29th September to 1st October 1981. This follows the 1977 conference on 'Bird of Prey Management Techniques', which was attended by ornithologists, vets and falconers from 20 countries.

Goshawk populations have recently increased in some parts of Europe, following restrictions on pesticide usage, and there is renewed controversy between hunting and protection interests about goshawk control. This conference will present recent research findings on goshawk population dynamics, predation and management, thus providing a basis for formal and informal discussion of how some of the conflicts might be resolved. The program will be of ½-hour papers by main speakers, with some shorter contributions and no late-night sessions! Proceedings will be published.

Those interested in giving papers or otherwise participating please contact: Dr. Robert Kenward, Institute of Terrestrial Ecology, Monks Wood, Abbots Ripton, HUNTINGDON, Great Britain.

Ingles, L. G. 1965. *Mammals of the Pacific states.* Stanford University Press, Stanford, CA 506 pp.

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THE LAYING OF REPLACEMENT CLUTCHES BY FALCONIFORMS AND STRIGIFORMS IN NORTH AMERICA

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Abstract

This paper discusses the laying of replacement clutches by North American raptors by reviewing existing literature and presenting data gathered from oological collections and from the double-clutching of wild and captive birds. We found that most species recycle; however, the frequency of recycling declined with an increasing stage of incubation. Clutch size did not decrease significantly between layings for most species. Although a single replacement clutch was usually laid, multiple replacements are known. After loss of the first clutch, raptors usually renested in the same site. If a new location was used, it was usually in close proximity to the original site. Although data from areas north of southern Canada were scarce, it appeared that recycling was rare in arctic regions. We concluded that double-clutching can be used in most management plans for North American raptors.

Introduction

That certain birds of prey possess the ability to lay an additional set of eggs after loss of their initial clutch has long been known (e.g., Wade 1882; Barlow 1897). Most early data on the laying of these replacement clutches were gathered by oologists who noted this occurrence after removing clutches (Bent 1937, 1938; Newton 1977). Replacement clutches have also been mentioned in more recent writings (Beebe 1974; Fyfe 1976; Newton 1977, 1979; Walton 1977). Replacement clutches, resulting from the practice of double-clutching, are now an important part of many propagation projects concerning raptors (Lejeune 1972; Fyfe 1976; Burnham et al. 1978). For double-clutching to be successful, however, data must be available on the response of the species to egg removal. Except for the Peregrine Falcon (*Falco peregrinus*), published data are scarce.

The purposes of this paper are to (1) summarize data in the literature on replacement laying and (2) present new information on this process gathered from oological collections and from the double-clutching of wild and captive birds. The scope of this paper is limited to data concerning mostly North American species. We hope this paper stimulates future work in the area of double-clutching in raptor management and encourages captive breeders to publish data they likely possess concerning replacement laying.

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Table 1. Summary of Data Concerning Various Aspects of Clutch Replacement by North American Raptors Based on Museum Records and Literature References (clutch size based on museum records only).

Species	Recycling time X	(N)	Range	No. known relayings	Clutch size (X;SD) First	Replacement	N	%change	Incubation stage	Nest sites	Dates (locations)	Sources and relevant literature
Barn Owl *(Tyto alba)*	20	(1)	-	1	5.0	4.0	1	nc[c]	Fresh	Same	Apr-May (CA)	1
Long-eared Owl *(Asio otus)*	18	(3)	12-22	1	6.0	6.0	1	nc	10%	Same	Mar-May (CA, OR)	1,24
Short-eared Owl *(A. flammeus)*	-	-	-	3	7-8	7-8	-	nc	-	Same	June (WA)	1
Screech Owl *(Otus asio)*	22	(2)	14-29	1	3.0	3.5	2	nc	Slight	Same	Apr-May (CA, OR)	1,24
Great Horned Owl *(Bubo virginianus)*	20	(12)	8-35	1	3.1 (0.94)	2.8 (0.98)	11	-9.7	to 14 days	Same-100m	Feb-Apr (TX,IA,AZ, CA,WY)	1,24,33
California Condor *(Gymnogyps californianus)*	37	(2)	33-41	1	1.0	1.0	2	nc	-	Captive	Apr (CA)	18
Black Vulture *(Coragyps atratus)*	26	(4)	25-27	2	2.0	2.0	4	nc	to 7 days	Same	Jan-Mar (FL)	1
Caracara *(Polyborus plancus)*	-	-	-	2	-	-	-	-	-	-	-	5
Osprey *(Pandion haliaetus)*	26	(3)	25-28	1	3.5	3.0	2	nc	Fresh	Same	Mar-June (NY, CA)	1,2,4,16,30
Mississippi Kite *(Ictinia misisippiensis)*	14	(1)	-	1	-	-	-	-	-	Same	-	1,4
White-tailed Kite *(Elanus leucurus)*	-	-	19-22	1	3.0	4.0	1	nc	-	New	Apr (CA)	1,3
Marsh Hawk *(Circus cyaneus)*	-	(1)	-	1	4.6	-	-	-	-	-	Apr-May (MI)	35
Bald Eagle *(Haliaeetus leucocephalus)*	38	(4)	27-60	1	3.0	2.0	1	nc	Advanced	Same	Dec-Feb (FL) May (CA)	1,4,13
Goshawk *(Accipiter gentilis)*	18	(1)	-	1	-	-	-	-	-	-	-	26
Cooper's Hawk *(A. cooperi)*	13	(2)	10-14[d]	1	5.0	5.0	1	nc	-	Same to "nearby"	May (CA)	4

(A. striatus)										100 m	(OI,PA,CI)	
Black Hawk *(Buteogallus anthracinus)*	-	-	-	2	-	-	-	-	-	New	-	28
Harris' Hawk *(Parabuteo unicinctus)*	23	(1)	-	2	3.0	3.0	1	nc	Started	"Nearby"	Mar-Apr (AZ)	1,34
Red-shouldered Hawk *(Buteo lineatus)*	24	(6)	19-30	1	2.7	2.0	3	nc	to 14 days	Same to "nearby"	Mar-Apr (CA,MI) Jan-Mar (FL)	1,4,36
Broad-winged Hawk *(B. platypterus)*	13	(4)	12-13	2	2.7	2.0	4	nc	to 7 days	Same to 200 m	May-June (CT)	1,7
Swainson's Hawk *(B. swainsoni)*	27	(2)	24-29	2 ?	3.0	3.0	1	nc	Heavy	Same to 200 m	Apr-July (TX)	1,22,25
White-tailed Hawk *(B. albicaudatus)*	13	(2)	10-15	1	2.0	2.0	2	nc	Fresh	Same to "nearby"	Mar-Apr (TX)	1,21
Red-tailed Hawk *(B. jamaicensis)*	17	(9)	12-25	1	2.8 (0.67)	2.1* (0.60)	9	-25.0	Slight	Same to "nearby"	Mar-May (PA,OR,CA,TX)	1,4
Golden Eagle *(Aquila chrysaetos)*	24	(10)	19-30	1	2.0 (0.00)	2.2 (0.42)	10	+10.0	One-half	Same	Feb-Apr (CA)	1,4,27
American Kestrel *(Falco sparverius)*	17	(17)	9-34	3	4.6 (0.92)	4.7 (0.47)	11	+ 2.2	Advanced	Same	Mar-May (CA)	1,23
Merlin *(F. columbarius)*	12	(1)	-	1	5.5	5.5	2	nc	Fresh	"Nearby" to 300 m	May-June (Albt. and Nfld., Can.)	1,5
Prairie Falcon *(F. mexicanus)*	16	(12)	13-25	1	4.9 (0.33)	4.4* (0.53)	9[a,b]	-10.2	14,16,18, 32 days	Same	Apr-May (CA)	1,5,9,29
Peregrine Falcon *(F. peregrinus)*	18	(8)	14-21	2	3.6 (0.55)	3.5 (1.00)	8[a]	-2.8	to 18 days	Same to 100 m	Apr-June (CA)	1,5,6,8,10, 11,12,14,15, 17,19,20,32

*P<0.05, t-test.

[a]Includes double-clutching experiments by B. Walton.

[b]Includes four clutches from captive birds.

[c]nc=not calculated.

[d]Includes wild pair observed by B. Walton in 1975.

Reference codes: 1-WFVZ, 2-Ames (1966), 3-Barlow (1897), 4-Bent (1937), 5-Bent (1938), 6-Bond (1946), 7-Burns (1911), 8-Cade and Fyfe (1970), 9-Dawson (1913), 10-Fyfe (1976), 11-Green (1916), 12-Herbert and Herbert (1965), 13-Herrick (1934), 14-Hickey (1942), 15-Hickey and Anderson (1965), 16-Kennedy (1977), 17-Keyes (1906), 18-Koford (1953), 19-Lejeune (1972), 20-Nethersole-Thompson (1931), 21-Nyc (1941), 22-Olendorff (1975), 23-Porter and Wiemeyer (1972), 24-Sclater (1912), 25-Sharp (1902), 26-Simpson (1909), 27-Slevin (1929), 28-Thomas (1908), 29-Tyler (1923), 30-Tyrrell (1936), 31-Wade (1882), 32-Walton (1977), 33-Wolfe (1912), 34-Mader (1977), 35-Craighead and Craighead (1956).

Methods

The data accompanying egg sets housed at the Western Foundation of Vertebrate Zoology (WFVZ) were studied; data transcribed included date and location of collection, clutch size, incubation stage, nest site, collector, and collector's comments. Because incubation terminology has not been standardized, date of set collection was corrected on the basis of reported incubation to give date of clutch initiation. Using the approximate incubation period of a species (Bent 1937, 1938; Brown and Amadon 1968; Newton 1977), the date of clutch initiation was estimated by subtracting stage of incubation in days from date of set collection (Anderson and Hickey 1970; L. F. Kiff, ms). Data gathered by Walton while experimenting with double-clutching wild and captive Peregrine and Prairie (*F. mexicanus*) Falcons are also presented.

To help standardize terminology, the following definitions were applied to several important terms: replacement clutch—the set of eggs laid following loss (natural or artificial) of a previous set (can apply to more than one replacement); double-clutching—the practice of removing a set of eggs with the purpose of initiating the laying of an additional clutch (i.e., the replacement clutch); recycling—the act of laying an additional set of eggs after loss of a previous set. The terms *set of eggs* and *clutch* are synonymous.

Results and Discussion

A summary of data (table 1) reveals the scattered nature of available information on recycling. It was evident, however, that most North American falconiforms and strigiforms recycled even when incubation was in an advanced stage; however, the frequency of recycling apparently decreased with an increasing stage of incubation (see also Green 1916; Hickey 1942; Craighead and Craighead 1956; Newton 1977). The upper limit on recycling appeared to be after about 25 days incubation, although recycling did occur after longer periods (table 1). In falcons, the frequency of recycling was highest if eggs were removed after 7 to 10 days of incubation (Fyfe 1976). No clear trends were shown when we correlated stage of incubation when eggs were lost with recycling time; this was not surprising given our relatively small sample sizes. It is likely that species-specific behavioral, physiological, and environmental controls of breeding are likely important in setting limits on recycling.

It appeared that clutch size decreased slightly with subsequent layings for most species. In those species with a relatively large sample size, only the Red-tailed Hawk (*Buteo jamaicensis*) and Prairie Falcon showed a significant decrease in clutch size between layings (table 1). In no case did clutch size decrease the equivalent of one egg. This should thus be considered a weak trend that varies among individuals of a species. While experimenting with double-clutching the Osprey (*Pandion haliaetus*), Kennedy (1977) found clutch size to be smaller (3.0 vs. 2.6 eggs) for the second clutch; however, hatching rate of second clutches exceeded that of single-clutched birds.

In reviewing recycling in various birds, Lack (1954) concluded that physiological exhaustion of the female was not responsible for a reduction in clutch size. He felt that other factors, especially reduced food availability as the season progressed, likely influenced the size of the replacement clutches. Prey abundance should thus be analyzed concomitantly with studies of double-clutching in raptors.

Most records (WFVZ data and literature sources) recounted the laying of a single replacement clutch; several cases of multiple replacements are known. In New York, Herbert and Herbert (1965) noted the laying of four clutches within a two-month period by a Peregrine Falcon. A captive American Kestrel (*F. sparverius*) laid five clutches within

a 61-day period; the first four clutches each contained five eggs, and the fifth clutch decreased to three eggs (Porter and Wiemeyer 1972). By removing each egg as it was laid, Wade (1882) was able to induce several Sharp-shinned Hawk (*Accipiter striatus*) to lay 15 to 18 eggs during a one-month period. It is evident that many raptors possess the potential to lay more than one replacement clutch in a season.

Loss of eggs usually did not cause a shift in nest site (table 1). If a new nest was constructed, it was usually within several hundred meters of the original site. Although we cannot know the exact effects that clutch removal has on the behavior of raptors, the lack of any overt response implies that only minor harm results; egg removal by man likely simulates natural egg loss. The role that time of season of egg removal has on nest site selection and breeding success needs study.

Hickey (1942) and Beebe (1974) stated that recycling does not occur at "high latitudes." However, data presented herein on the Merlin (*F. columbarius*) showed recycling to take place in Newfoundland. Peregrine Falcons are known to recycle in Alberta (Cade and Fyfe 1970) and in the Queen Charlottes (Cade 1960), Canada, whereas in the arctic renesting is not likely to be successful (Cade 1960). The Bald Eagle (*Haliaeetus leucocephalus*) nesting in Alaska did not recycle after loss of eggs (Hensel and Troyer 1964). This was also true for eagles in the Aleutians (52° N. Lat.) when eggs were lost only 5 days after clutch completion (C. M. White, pers. comm.). The frequency of recycling apparently declines north of the southern tier of Canadian provinces. Studies such as those of Cade (1960), in which the onset and duration of the breeding cycle can be related to latitude, are needed prior to initiation of any raptor management plan that involves recycling.

Newton (1977) stated that recycling was relatively infrequent among buzzards and kites, and rare among eagles. Beebe (1974) felt that Bald Eagles would not recycle in the same season. Although results of this study show that these species do recycle, the relative frequency of recycling must remain speculative until additional data are collected. However, there is the possibility that double-clutching can be used as a method of increasing productivity in both species of North American eagles.

Except for Prairie and Peregrine Falcons, information presently available does not allow a description of the optimal stage of incubation or breeding season to initiate recycling. Data do show that double-clutching can be employed in most, if not all, management plans concerning North American falconiforms and strigiforms.

Acknowledgments

We wish to thank Lloyd Kiff, William J. Mader and Dan Warrick for commenting on this manuscript. We also thank Sherry Morrison for preparation of several drafts. This project was supported in part by the Western Foundation of Vertebrate Zoology.

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PROBABLE PREDATION ON WHITE-TAILED KITE BY RED-TAILED HAWK

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Though Red-tailed Hawks (*Buteo jamaicensis*) may prey upon a variety of both vertebrate and invertebrate animals (Sherrod 1978), reports of their predation on raptors are apparently rare. Drawing from a handful of observations, classical summaries of the Red-tailed Hawk's diet include Red-tailed Hawk, Red-shouldered Hawk (*Buteo lineatus*), and Screech Owl (*Otus asio*) as known prey (Bent 1937; Fitch et. al. 1946). More recently, cannibalism involving adult Red-tailed Hawks was reported by Clevenger and Roest (1974).

On 2 January 1978, the freshly killed carcass of a White-tailed Kite (*Elanus leucurus*) was found on the ground at the entrance of Armand Bayou Nature Center in southeast Harris County, Texas, in a spot from which a large Red-tailed Hawk had flown only moments before. The head had been completely removed and apparently eaten; only the lower mandible and a single quadrate bone remained. The furcular area had been cleared of tissue through the breast muscles to the sternum. Many dorsal feathers had been removed and lay scattered around the carcass. The otherwise intact carcass was salvaged and placed in the Texas Cooperative Wildlife Collections at Texas A&M University, College Station (TCWC, No. 10418). The kite was an adult female.

We did not see the actual kill but assume that it was predation and not scavenging for the following reasons. First of all, it seems unlikely that the hawk discovered a kite

wounded by gunshot because the carcass was well within the boundaries of the nature center where firearms are prohibited. In addition, no evidence of gunshot wounds was discovered in the examination of the carcass. Secondly, internal examination revealed that the vertebral column, as well as several vertebral ribs on the left side, had been broken in the thoracic region. Such damage probably resulted from a single impact of great force from above, as by a hawk in a dive. It seems improbable that such localized heavy damage would have resulted had the kite been wounded and the encounter taken place on the ground. An alternate explanation, that the hawk was scavenging on a road-killed kite, is not feasible because the prey bird was discovered freshly killed across a drainage ditch and up a steep embankment from the nearest road.

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GOLDEN EAGLES SUCCESSFULLY BREEDING IN SUBADULT PLUMAGE

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In 1979 I observed a pair of breeding Golden Eagle (*Aquila chrysaetos*), in Carbon County, Wyoming, in which one bird was in subadult plumage. This pair successfully raised and fledged two young. I observed and photographed these birds periodically for seven weeks. The fact that eagles were breeding in subadult plumage is significant in that most eagles do so only under conditions which are unusually favorable or unfavorable (e.g., during heavy persecution). Other species of raptors breed at ages younger than usual when conditions are exceptionally good, either in extremely favorable years or areas; or when there are fewer than usual adults in a population leaving territories vacant (Newton 1979). In the Prairie Falcon (*Falco mexicanus*) it was observed that 9 percent of a population bred in subadult plumage (all female), and 8 out of 10 successfully fledged at least one offspring (Platt 1979 and pers. comm.).

In the European Sparrowhawk (*Accipiter nisus*), Goshawk (*Accipiter gentilis*), and Kestrel (*Falco tinnunculus*), the percentage of females breeding in subadult plumage was directly correlated with prey abundance and scarcity (Newton 1979, McGowen 1975, and Village 1979). Both sexes in pairs of Golden Eagles have been observed in immature plumage, and young have been raised in some instances (Sandman 1957, Bates 1976). In Scotland Golden Eagles, when both birds were in subadult plumage, have

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formed pairs, defined territories, and constructed nests with no young produced in most cases. This was in an area of high persecution with a small or nonexistent "floating" population of nonbreeding adults.

Bates (1976) observed successfully breeding pairs in Scotland in which he believed the male to be the subadult. Jollie (1947) reports that "the plumage achieved by the second molt may be called 'subadult' because I believe that I have observed birds breeding in this plumage and because it introduces the first feathers of the adult pattern." Assumption of adult plumage does not necessarily mean that an eagle is sexually mature and can breed though we usually assume it, i.e., Spanish Imperial Eagle (*Aquila heliaca*) (Brown 1976). I am unaware of any other published references to Golden Eagles successfully breeding in subadult plumage; however, this may be a more common phenomenon than is represented by the literature.

Michael Kochert (pers. comm.) of the Bureau of Land Management, Boise District, Idaho, reports that 12 Golden Eagles, one individual per pair, in 564 nesting attempts (2%) were subadults. They colormarked the birds according to size and behavioral observations (incubation, etc.) to distinguish between the sexes. He believes that the subadults were all males.

During 40 years of observations, Morlan Nelson (pers. comm.) noted subadults were approximately 1–2 percent of the breeding population. He estimates an average success rate of 80 percent for these birds. He observed more female immatures at nests but feels more studies are needed on differences in mature feathers between the male and female. There is a distinct difference in the moult. Males produce mature feathers a year or more earlier than females, according to Nelson.

I returned in 1980 to the same nest site in Wyoming, and there were two adult Golden Eagles occupying the nest. I have no direct information that they were the same birds.

Acknowledgments:

I gratefully acknowledge the aid and expertise of E. Allen, Colorado Division of Wildlife; R. Johnson, M. Kochert, J. R. Murphy, M. Nelson, S. and P. Platt, C. M. White, and R. Williams.

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COYOTE STEALS SNOW GOOSE FROM BALD EAGLES

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All the larger African carnivores, except the cheetah, steal meat from others at one time or another (Curio 1976). There are also numerous accounts of birds stealing from other birds (kleptoparasitism), and at least 12 species of birds are known to have stolen food from mammals (Brockmann and Bernard 1979). However, we have been unable to find any accounts in the literature of mammals robbing birds. In November 1977 two of us (SDP and RAW) witnessed such an incident at DeSoto National Wildlife Refuge located on the Missouri River in Harrison County, Iowa, and Washington County, Nebraska.

Shortly after dawn on 12 November we were watching with spotting scopes a group of about 30,000 of the Snow Goose (*Anser caerulescens caerulescens*) feeding in a harvested cornfield. At about 0700 the geese had flown from the refuge lake to the cornfield, a distance of about 1 km. At 0715 the flock arose en masse, circled a few times, and flew off. We then noticed 5 immature Bald Eagle (*Haliaeetus leucocephalus*) standing where the geese had been feeding. Among the eagles was a mature Snow Goose (blue phase plumage) obviously disabled and unable to fly or walk. The eagles maintained varying distances from the goose, from a minimum of about 2 m to a maximum of about 30 m. We had not seen the eagles earlier, perhaps partly because of poor light conditions. We assumed the eagles came from a grove of trees about 500 m away where eagles commonly roosted although we did not see their approach.

At 0730 a coyote (*Canis latrans*) approached the group across the open field. The coyote picked up the goose, which was still alive, and moved 200–250 m to an area near tall grass and unharvested grain. The coyote then dropped the goose, which appeared to be dead. A second coyote emerged from the tall vegetation, picked up the goose, and disappeared into the vegetation. There was no obvious behavioral interaction between the coyotes during the transfer of the goose, and they did not approach each other closer than 5 m.

At 0734 the first coyote again approached the group of eagles. Three took flight and began to dive at the coyote. Whenever they flew close, the coyote lunged and snapped at the eagles. The coyote soon began a series of nose-to-the-ground searching movements in the area where the goose had previously been captured. There was no apparent interaction between the coyote and the two eagles remaining on the ground. At 0737 the coyote moved briefly to the tall vegetation but soon returned and continued its

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searching in the cornfield. The eagles in the field then took flight and left the area. At 0742 the coyote returned to the tall vegetation and disappeared. We searched the tall vegetation on foot but found no trace of the goose.

Since we were unable to recover the remains of the goose, it was impossible to determine whether the goose was initially disabled by the eagles. However, we believe that this is what happened because the goose had flown from the lake to the field; no geese were in the field prior to 0700. Geese do not remain in fields overnight at DeSoto Refuge because of harassment and possible predation by coyotes. Sick or crippled geese that cannot reach the safety of the lake are soon scavenged by coyotes.

Although Bald Eagles are seldom seen taking healthy waterfowl, Bent (1938) reported that waterfowl are important in the diet of Bald Eagles in certain seasons.* Brewster (1880) and Meinertzhagen (1959) also reported that Bald Eagles attack waterfowl, including wild geese, in flight and on water. One of us (EEK) observed an immature Bald Eagle kill a live female Mallard (*Anas platyrhynchos*) that was loafing on the shore of the frozen refuge lake with a flock of about 100 on 26 December 1977. The eagle approached the ducks by gliding along the shoreline about 2 m above the ground. Presumably, this low-level flight allowed the eagle to surprise its prey without being silhouetted against the sky. The eagles undoubtedly approached the geese with a similar low-level flight pattern that also eluded the notice of the human observers.

We have observed that snow geese usually take flight when an eagle (or airplane) flies overhead. Such behavior may be conditioned by repeated threats from avian predators. Bald Eagles are common at DeSoto Refuge during fall and winter, and coyotes are common as permanent residents. Both coyotes and eagles feed extensively on carcasses of geese and other waterfowl that die from gunshot wounds or disease. Ordinarily, eagles are diurnal feeders, and coyotes are usually nocturnal. Interactions between the two are uncommon. Thus, this kleptoparasitic act was probably a chance encounter in which the coyote capitalized on a fortuitous feeding opportunity.

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*Ed. Note: Bald Eagles certainly do take numbers of healthy waterfowl, including geese, and waterfowl-sized sea birds in the Aleutian Islands; see Sherrod S. K., C. M. White, and F. S. C. Williamson, *Living Bird* 15:143–182, 1977.

SPATIAL DISTRIBUTIONS OF AMERICAN KESTRELS AND LOGGERHEAD SHRIKES WINTERING SYMPATRICALLY IN EASTERN TEXAS

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American Kestrels (*Falco sparverius*) and Loggerhead Shrikes (*Lanius ludovicianus*) are facultative insectivores feeding mostly on grasshoppers. They switch to small mammals and small birds when low temperatures reduce insect activity. Both hunt primarily from exposed perches such as utility lines and poles, although kestrels scan for prey while hovering (Bent, *U.S. Nat. Mus. Bull.* 170, 1938; Bent, *U.S. Nat. Mus. Bull.* 197, 1950; Roest, *Auk* 74:1–19, 1957; Balgooyen, *Univ. Calif. Pub. Zool.* 103:1–88, 1976). Superficially, sympatric kestrels and shrikes would appear to compete for food. In this note we show that kestrels and shrikes exhibit spatial segregation.

During December 1977, we recorded the sequence of occurrence and the location to the nearest 1.6 km (1 mile) of 151 kestrels and 249 shrikes censused along a 1464-km (910-mile) automobile survey route in eastern Texas. Most of the birds were perched on utility lines when sighted (92% of kestrels; 98% of shrikes). To determine whether the numbers of individuals of each species locally were correlated, we ascertained the number of individuals of both species in each of the 91 16-km segments of the survey route. Kestrels averaged 1.66 ± 2.46 birds per 16 km and were present in 51 of the segments, and shrikes averaged 2.74 ± 3.40 individuals per 16 km and were present in 64 segments.

For both kestrels and shrikes the number of birds seen per segment was positively, though not significantly, correlated with the number of individuals of the other species present in the segment ($r = +.26$, d.f. $+ 1$, $.10 > P > .05$, for kestrels; $r = +.23$, d.f. $= 1$, $.10 > P > .05$, for shrikes). While a negative correlation between the two species per 16-km interval might indicate one species depressing numbers of the other, the positive correlation we found most likely reflects similarity in habitat selection along our rather heterogeneous survey route, and does not exclude the possibility of competitive depression.

An analysis of the sequence of kestrel and shrike sightings along the survey route revealed that in both species conspecifics tended to occur together (table 1). In 60 percent of the instances involving sequential sightings of kestrels and 83 percent of the instances involving sequential sightings of shrikes, three or more conspecifics were viewed in succession. This indicates that the clumping we saw was not simply the result of mated pairs occurring together.

Taken as a whole, these results show that while the two species did occur together, they were not randomly distributed with respect to each other. What remain to be determined are the habitat parameters along which the two species partitioned resources and whether that partitioning was affected by interspecific social dominance (sensu Morse, *Amer. Nat.* 108:813–830, 1974).

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This work was supported by the Ohio State University Department of Zoology and College of Biological Sciences.

Table 1. Statistical Analysis of the Sequence of American Kestrel and Loggerhead Shrike Sightings along a 1464-km Eastern Texas Survey Route.

Species		Followed by		P[a]
		American Kestrel	Loggerhead Shrike	
American Kestrel	observed	81	70	<.005
	expected[b]	56.8	94.2	
Loggerhead Shrike	observed	68	180	<.005
	expected	93.9	154.1	

[a]Chi-square test for goodness of fit.
[b]Based on random sequence.

BOOK REVIEWS

Animali in pericolo in Italia. 1976. Franco Pedrotti (ed.). Camerino: Italian World Wildlife Fund. 710 pp., 119 plates, 154 figures.

Little is known of Italian ecological research outside Italy itself. This volume provides an excellent opportunity to discover the high quality and professionalism of field research conducted by Italian researchers on endangered species. The Italian section of the World Wildlife Fund has financed and organized a limited number of research projects in Italy since 1967. This book contains 20 papers, most of which analyze the results of up to 10 years of field research on the small number of Italian bears, wolves, moufflons, vultures, eagles, ungulates, and frogs. Four of the papers deal with the ecology and distribution of rare animals in the Abruzzo National Park.

Eight papers deal with Italian raptors, usually reporting and analyzing the results of field studies. The first concerns the historic and present status and migration of the Egyptian Vulture (*Neophron p. percnopterus*). The author, G. Bologna, has organized a census of it in Italy from 1971 to 1976. This vulture occurs year-round in Sicily with a breeding population of 40–50 vultures. On the Italian mainland it is confined to the southern half as an uncommon summer resident (breeding population of 70–80 vultures). The species is threatened, and the author suggests strict protection and law enforcement, creation of special nature reserves around nesting areas, and the establishment of "vulture restaurants."

M. Chiavetta discusses the distribution and nest site selection of Italian Peregrine (*Falco peregrinus*) and Lanner Falcons (*F. biarmicus*). He compares the historic, present, and potential breeding density of both species in a study area, the Apennine Mountains, state of Emilia-Romagna (near Bologna). Nice drawings of cliff cross-sections and a distribution map of falcon nest sites, 1971–1974, complement this study. With a combination of personal travel (80,000 km), reports of hunters, and extrapolation techniques, he estimates the total population of the Peregrine in Italy at around 300–400 pairs

(mostly islands and coastal habitats), and of the Lanner to reach 150–200 pairs (2/3 in the four southernmost states) in 1975.

The next paper by B. Massa summarizes what is known of the biology of Bonelli's Eagle (*Hieraaetus f. fasciatus*) and should be valuable reading for anybody interested in this widespread Old World eagle. There are fewer than 10 pairs left in Sicily and about 30 pairs in Sardinia. The only personal field data in this report concern human impact. The article contains eight excellent plates from this eagle's nest in southern Spain by P. Van Groenendall and W. Suetens.

The ecology and the breeding success of the Goshawk (*Accipiter gentilis*) in the *Karst* region of Trieste in northern Italy was studied between 1966 and 1976 by F. Perco. Many broods were lost because of human impact. The fledgling rate was only 26.3 percent (10 fledglings out of 38 hatched eggs). The principal prey species among a relatively small prey sample examined (n=54) was the European Jay (*Garrulus glandarius*), which constituted 46.2 percent of all prey. The home range of the breeding population was estimated at 1,400–2,200 hectares in a highly disturbed region with a human population density of about 1,400 persons/km^2.

A paper by F. Petretti deals with the breeding ecology of a pair of Black Kites (*Milvus migrans*) in the marshes near Rome, probably the first such study from southern Europe. He reports on daily activity cycles (two strong peaks in the morning and in the late afternoon), on the electrocution of a fledged Black Kite, and on the prey spectrum (85% fishes).

The most interesting raptor paper in this book concerns the behavior and ecology of a pair of Golden Eagles (*Aquila chrysaetos*) in the Apennine Mountains of Umbria. Unfortunately, author B. Ragni uses a literary, anecdotal approach that makes reading difficult and time-consuming for this foreign reader. The observed eagle pair raised 77 eaglets over a period of just six years (1971–1976), an exceptionally high breeding success for this species. The main prey consisted of hares (*Lepus europaeus*).

During the winter months the adult male drove off the juvenile eagles from his territory. The male was the sole hunter during the breeding season. The eagle pair separated temporarily in late summer and fall; the adult male remained in the territory while his mate became the most solitary member of the family. The author includes good sketches of eagle behavior, and witnessed a number of remarkable happenings, including the male's attack on a glider.

Finally, there is the excellent article by H. Schenk (a vulture specialist) on the faunistic situation on the large Tyrrhenian island of Sardinia. The status, history, and prognosis for the future is treated for the Cinereous Vulture (*Aegypius mouachus*), the Griffon Vulture (*Gyps fulvus*), the Bearded Vulture (*Gypaetus barbatus*), and several eagles, hawks, harriers, and falcons. All accounts are accompanied by good statistical data and distribution summaries.

Hartmut Walter

Hiraldo, F., Delibes, M., & Calderon, J. 1979. El Quebrantahuesos *Gypaëtus barbatus* (L.). Sistematica, Taxonomia, Biologia, Distribucion, y Proteccion. Inst. Nac. para la Conserv. de la Naturaleza, monogr. No. 22. 183 pp. (available from Servicio de Publicaciones Agrarias, Paseo de Infanta Isabel, 1. Madrid-7.)

This exciting monograph on the Bearded Vulture (*Gypaëtus barbatus*) is a required reading for all vulture specialists and thought-provoking for other raptor students. Chapter 1 is on the "bonebreaker's" morphology (little sexual dimorphism; males are

slightly smaller). The largest size belongs to specimens from Central Asia, the smallest to the Ethiopian population, a cline following Bergmann's ecogeographical rule. The authors suggest a taxonomical revision reducing the number of subspecies to only two on the basis of a combination of size and plumage characters: *G. b. barbatus* of Eurasia and northern Africa, and *G. b. meridionalis* of eastern and southern Africa. Succeeding chapters deal with territoriality, food requirements, and the entire reproductive cycle. There is a wealth of data on metabolic needs and geographical variation of egg size. After a general status survey (fig. 28 should include Sardinia as a breeding habitat) the question is posed: Why is the Bearded Vulture disappearing? Various direct and indirect human impacts have caused the death of many adult birds, raising the otherwise very low natural mortality rate among adults. Since sexual maturity is reached at the age of 5 or 6 years, and the chances of a fledged bird to reach maturity are rated below 10 percent, the annual recruitment into the breeding population is too low to compensate for the much larger loss of adults.

The last chapter deals with the conservation measures on the Iberian Peninsula to protect the existing breeding areas and populations and to revitalize former breeding locations. First, protection of existing breeding nuclei has to be effective, absolute, and well coordinated among all administrative agencies involved in the effort. Second, recolonization requires human assistance, in this case the transport, care, and release of young Bearded Vultures (probably from the Pyrenean population) into suitable historic breeding habitats.

This monograph has a soft cover, 21 tables, 35 figures, and a large number of typing errors. The latter can be found and corrected with a special error data sheet. The English summary is excellent. It covers chapter by chapter and makes it relatively easy for the non-Spanish reader to extract the important materials from this modern study, a true testimonial of the quality of raptor research in Spain today.

Hartmut Walter

Feeding ecology and niche differentiation in Goshawk (*Accipiter gentilis* L.) and Sparrowhawk (*Accipiter ninus* L.). P. Opdam. Drukkerij Presikhoof, Ruitenbergloan 29, Arnhem, The Netherlands. 91 pp., paper, price not given, obtainable from Rijksenstituut Voor Natuurbeheer, Leersum-Uasteel, Broehhuizen, The Netherlands (in English with Dutch summary).

This volume represents the collected papers of Paul Opdam, brought together in one volume, with J. Thissen, P. Verschuren, and G. Muskens coauthoring some of the Goshawk material. There are seven chapters of which three have been previously published in European journals. (A seventh chapter consists only of a Dutch summary.) Chapter 1 is an introduction to the overall theme of the study, which is to test Gause's principle and to compare the feeding ecology of these two raptors to see if intra- and interspecific differences in body size are correlated with differences in food. Chapter 2 describes the feeding ecology of a population of Goshawks on either side of the Dutch-German frontier over the 1969–1973 period. This paper was previously published in *J. Ornithol*, 118 (1):35–51, 1977. Perhaps the salient finding was that although at least 72 identifiable species showed up as food, the bulk of the remains consisted of only five species. These latter species were related to an environment created by modern man's agricultural practices and the breeding and racing of homing pigeons. Twenty-two species were recorded as prey items only once in the four-year study. The Goshawk population dis-

cussed is one of the most dense in Europe, again correlated with a landscape managed intensively for agriculture.

Chapter 3 (previously published in *Ardea*, 66:137–155, 1978) treats Sparrowhawk feeding ecology in a fashion similar to that of the Goshawk in chapter 2. The proportion of prey from three different categories (field, village, and forest species) are compared for each season. Like the findings on Goshawks, although over 100 prey items were identified, only nine species made up about 70 percent of the food items. Chapter 4 (previously published in *Ardea*, 63:30–54, 1975) then brings together data from both studies to present a comparative picture of sex, species, and temporal differences between them in sympatric areas that tend to lead to both intra- and interspecific partitioning of resources. For example, in winter the family turdidae made up less than 10 percent of the Goshawk food but more than 20 percent of the combined Sparrowhawk food; within the Sparrowhawks, males took only 6 percent of their food fare from turdidae, but females' diet was more than 58 percent turdidae. On the other hand, the family columbidae made up less than 1 percent of the Sparrowhawk food and 70 percent of Goshawk food. Female Goshawk take of Domestic Pigeon (*Columba livia*) was only 21 percent, and that species made up 40 percent of male Goshawk food. Opdam concluded that each accipiter "group" (each sex by species) occupied a somewhat different niche, with intraspecific overlap more extended than interspecific overlap. The niche-breadth decreased under poor (in winter) food conditions.

The new material in the publication comes in chapters 5 and 6 and apparently represents a heretofore unpublished analysis by Opdam. Chapter 5 is titled "Niche utilization in coexisting accipiter species." He raises several questions regarding the number of accipiter species that can coexist and whether the "accipiter niche" space in western Europe is sufficiently occupied that a third species cannot also coexist with the two there. The Levant Sparrowhawk (*A. brevipes*) comes closest geographically to being a third accipiter in western Europe. The main purpose of his discussion is not to solve any problems relating to his question but to indicate fields of research wherein these questions might be answered.

For some of the analysis in chapter 5, prey items are classed into 13 size groups. Unfortunately we are not told what the size groups are other than that size groups 3–4 correspond to the weight of male Sparrowhawks, group 6 to the weight of female Sparrowhawks, and group 10 to the weight of male Goshawks. Some prey sizes are exploited 2–3 times more than others, and those most heavily used correspond to the weight of the accipiter sex that catches it. Opdam suggests that certain sized prey might include many species of high vulnerability and that the frequency of that size class in the food items simply outnumbers the low vulnerability species and thus accounts for the correlation. Plotted values on the mean body weight of the two western European and largest and smallest North American accipiter against mean body weight of their respective prey fits a straight line. The middle-sized North American accipiter (Cooper's Hawk *A. cooperi*) deviates from this line suggesting to Opdam that mean prey size is also governed by factors other than size of the predator. Finally Opdam suggests that the reason only two accipiters are sympatric in western Europe while three are in North America is that in North America the distribution of birds weighing up to his size class 8 differs from Europe in such a way that the niche-space of *A. ninus* can be occupied by two species i.e. *A. striatus* and *A. cooperi*. His discussion of coexisting accipiters in other parts of the world is provocative, especially concerning the tropics.

The final chapter is entitled "Sexual Size Dimorphism and Feeding Ecology in Birds of Prey with Special Reference to Goshawk and Sparrowhawk." Three general categories of theories on sexual dimorphism are broached, namely, (1) niche-differentiation hypothesis, (2) ethological-function hypothesis, and (3) hypotheses emphasizing energetic advantages for efficient foraging during reproduction. These hypotheses each incorporate the main questions, Why do the sexes differ in size? Why do the species differ in the amount of dimorphism? Why is the female the largest? Opdam's discussion on the niche-differentiation hypothesis, for accipiters at least, concludes it is unikely that for Goshawks and Sparrowhawks food will regularly be in short supply during the breeding season whereas during winter limited food may cause competition and reinforce size differences. His analysis supports the conclusion that bird-eating accipiters show the greatest dimorphism, and reptile, amphibian, or insect eaters least. Twelve forms of predominantly bird-eating accipiters had an average sexual dimorphism index of 15.8 percent, 12 forms with mixed prey choices an index of 12.4 percent, and 6 species of predominantly reptile, amphibian, insect, or small mammal eaters an index of 8.5 percent. Opdam then points out problems or exceptions to the three main hypotheses centered around the ethological function proposals for dimorphism and the four main hypotheses that argue for an energetic benefit to sexual dimorphism.

In conclusion, he postulates that for *A. nisus* and *A. gentilis,* and perhaps the entire genus *Accipiter,* the following four processes determine dimorphism: (1) intraspecific competition for food resulting in sexual size differences, (2) interspecific competition for food to help set limits to the amount of dimorphism, (3) different mortality rates resulting from intraspecific niche differences also helping to set limits to the amount of dimorphism, and (4) energetic factors setting limits to the amount of dimorphism. The one glaring error is the spelling *tung* for *tongue,* but this volume is certainly a contribution to the library of any serious student of falconiforms.

C. M. White

ABSTRACTS OF THESES AND DISSERTATIONS

THE ECOLOGY AND STATUS OF THE HARRIS' HAWK (*PARABUTEO UNICINCTUS*) IN ARIZONA

Abstract

The Harris' Hawk was studied in Arizona from January 1976 to October 1977. Its past and present status and distribution are described. Where two separate populations once resided in Arizona, one now remains and occupies 3,880 sq km of the Arizona Upland subdivision of the Sonoran Desert.

Nests were built or old nests repaired from January to August, and eggs were set from mid-January to mid-August. Extra clutches were documented in fifty nesting ranges. Occasionally second clutches were laid befoe young of first broods were fledged. Fledging dates ranged from April to October. At nine locations active nests were .8 km apart, and at two locations nests were just .5 km apart. Within two study areas nesting density was 2.5 sq km per active nest. The mean distance between nests was 1.8 km. In 1977 Harris' Hawks reoccupied 91 percent of the nesting ranges used in 1976. More than two adults were observed at 46 percent of 227 nesting ranges.

Productivity was ascertained for 396 nesting attempts. The average clutch contained 3.16 eggs (range 1–5) and an average 1.62 young fledged per nesting attempt. Seventy-four percent of the nesting attempts were successful.

Food habits, mortality, and factors influencing frequency of double broods and the

timing and longevity of the breeding season are discussed. The pejorative implications of excessive disturbance to nesting birds, habitat loss, and electrocution mortality are discussed. Management recommendations are given.

Literature Cited

Whaley, W. H. 1979. The ecology and status of the Harris' Hawk (*Parabuteo unicinctus*) in Arizona. M.S. thesis, University of Arizona, Tucson. 119 pp.

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ECOLOGY AND BEHAVIOR OF THE GYMNOGYNE (*POLYBOROIDES TYPUS*)

Observations made during this study provided data on general nesting biology, parental behavior, and feeding ecology of two pairs of Gymnogyne or African Harrier Hawk (*Polyboroides typus*) throughout most of the 1978 breeding season. The nests were attended by at least one of the pair 98 percent of the daytime, with both parents participating in the 35–36-day incubation period. Changes in facial color and exchange of nesting material were apparently stimuli necessary for cooperative transfer of egg possession during incubation. After chicks had hatched, the male returned to the nest only to deliver prey to the female. Changes in male's facial color were also incorporated into food transfers. By the fourth week the female began hunting, and the male no longer approached the nest but transferred prey to her away from the nest site.

Four general hunting methods were used: low soaring, high soaring, perch hunting and canopy-ground hunting. Of 85 prey items identified during this study 33 percent were birds (primarily nestlings), 41 percent reptiles and amphibians, 15 percent small mammals, and 11 percent insects. Most prey can be characterized as defenseless or inactive at the time of capture.

The Gymnogyne is characterized by some specialized morphological adaptations: long, broad wings and tail; lightweight body; long tarsi; modified intertarsal joint; and a bare-faced, diminutive head. The unfeathered facial skin changes color ranging from light yellow to dark red. I hypothesize that these traits reflect behavioral adaptations relating to hunting and communication. The objectives of this study were to describe hunting strategies; identify prey captured; study behavior associated with changes in coloration of the adult facial skin (hereafter referred to as flushing); and describe parental activity and characteristics of the nesting cycle.

Prior to this study the most detailed record of the Gymnogyne was based on scattered observations in Kenya. Other reports in the literature are generally anecdotal. The Gymnogyne is most common in tropical western Africa, but its distribution includes sub-Sahara woodland habitats south to the Cape of South Africa (Brown and Amadon 1968).

Literature Cited

Thurow, Thomas L. 1979. Ecology and behavior of the Gymnogyne (*Polyboroides typus*). M.S. thesis, Brigham Young University, Provo, Utah. 28 pp.

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